tially continuous compared to many of the habitats they colonize in inland succession. Even if relatively small, coastal subpopulations may have been crucial links in spread and survival of their species.

ACKNOWLEDGMENTS

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REVISION OF PECTIS SECT. HETEROPECTIS (COMPOSITAE: TAGETEAE)

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Pectis L. sect. *Heteropectis* A. Gray is one of the smallest and most geographically restricted sections of *Pectis*. Comprising only two species, sect. *Heteropectis* is centered in the Sonoran Desert and only slightly exceeds the boundaries of that zone. No other section of the genus is known to occupy such a limited geographical range.

A unique feature of sect. *Heteropectis* is the structure of the pappus awns, which are unlike those of any other taxon in the genus, or indeed, in all of the Tageteae. The awns are retrorsely barbed in a manner similar to that of the pappus awns of *Bidens* (Heliantheae: Coreopsidinae). In *Bidens,* the barbed awns are an adaptation that promotes fruit dispersal by animals (Daubenmire, 1974). The pappus of the species of sect. *Heteropectis* may reflect a similar adaptation.

Taxonomic History

Gray (1849) originally described *Heteropectis* as a subgenus of *Pectis* and incorporated into this subgenus four species with aristate pappus: *P. coulteri* Harv. & Gray, *P. fastigiata* A. Gray, *P. filipes* Harv. & Gray, and *P. multiseta* Benth. In 1852, Gray amended his concept of *Heteropectis* by removing *P. fastigiata* and *P. filipes* and restricting it to taxa with retrorsely barbed pappus awns. At the same time, Gray also reduced *Heteropectis* to sectional rank with two species. In 1883, Gray further reduced *Heteropectis* by submerging it within sect. *Pectidium* (Less.) A. Gray. Fernald (1897) restored *Heteropectis* to subgeneric rank with three species: *P. coulteri, P. multiseta,* and the newly described *P. ambigua.* Rydberg (1916), although not recognizing infrageneric taxa other than species, grouped together four species referable to *Heteropectis: P. ambigua, P. bennettii* Klatt, *P. coulteri,* and *P. multiseta.*

The rank and circumscription of *Heteropectis* used in the present revision is based upon the emended concept of Gray (1852). Because the differences among various infrageneric species groups in *Pectis* seem insufficient for the establishment of subgenera, I am recognizing the sectional rather than subgeneric level for *Heteropectis* and similar taxa within the genus.

Chromosome Studies

Chromosome counts of $n = 12$ are reported here for the first time for all three taxa of sect. *Heteropectis* (Table 1). These new reports agree with the base chromosome number reported from species of other sections of the genus (Johnston and Turner, 1962; Keil, 1973). Apparently speciation in sect. *Heteropectis* has occurred entirely at the diploid level.

Sectional Relationships

Section *Heteropectis* is probably closely related to the larger and more widespread sect. *Pectothrix* A. Gray. Members of both sections are evolutionarily advanced taxa that are similar both morphologically (size, habit, head shape and size) and ecologically (emphemerals of desert regions). This similarity probably represents both parallel selective pressures and a common ancestry. Both sections were probably derived originally from ancestors that would be referable to a third section, *Lorentea* A. Gray. Some members of sect. *Lorentea* [e.g., *P. saturejaoides*

TABLE 1. NEW CHROMOSOME COUNTS FOR TAXA OF PECTIS SECT. HETEROPECTIS. Counts for *P. multiseta* var. *multiseta* and var. *ambigua* were made by Dr. A. M. Powell.

Pectis coulteri Harv. & Gray
Sonora, 14.8 mi E of Bahia de Guaymas, *Keil and Canne 8638B* (OS), $n = 12$; 7.2 mi SE of Navojoa, *Keil and Canne 8728* (OS), $n = 12$; 27 mi SE of Navojoa, *Keil and Canne 8734* (OS), $n = 12$.

Pectis multiseta Benth. var. *multiseta*
Baja California Sur, 7 mi W of La Palmilla, *Sikes and Babcock 243* (TEX), $n = 12$; 10 mi W of La Palmilla, *Sikes and Babcock 245* (TEX), $n = 12$.

Pectis multiseta Benth. var. *ambigua* (Fern.) Keil
Baja California Sur, 25 mi N of Todos Santos, *Sikes and Babcock 260* (TEX), $n = 12$; 26 mi N of Todos Santos, *Sikes and Babcock 261* (TEX), $n = 12$; 5 mi N of San Antonio, *Sikes and Babcock 267* (TEX), $n = 12$; 78 mi N of La Paz, *Sikes and Babcock 274* (TEX), $n = 12$.

(Mill.) Sch. Bip.] exhibit several features that are probably primitive in the genus (perennial habit, setose pappus, indefinite ray floret number, relatively mesic habitat). Section *Heteropectis* and sect. *Pectothrix* probably arose independently from different members of sect. *Lorentea.*

TAXONOMIC TREATMENT

PECTIS L. sect. HETEROPECTIS (A. Gray) A. Gray, Smithsonian Contr. Knowl. 3(5):83. 1852.—*Pectis* L. subg. *Heteropectis* A. Gray, Mem. Amer. Acad. Arts 4:62. 1849. Type species not designated. Lectotype (here chosen): *Pectis coulteri* Harv. & Gray.

Plants low, bushy, more-or-less pubescent, annual herbs, often strong-scented. Stems 1–35 cm long, much-branched. Leaves linear to oblong or narrowly obovate, bristly-ciliate on the margins, sometimes nearly to the apex, dotted on the undersurface with oil glands. Heads peduncled, solitary or in cymose clusters. Peduncles slender, bractless. Involucres cylindrical to campanulate. Phyllaries 5, linear to obovate, strongly keeled, dotted with oil glands. Ray florets 5; corollas yellow, with glabrous ligules and slender, glandular-puberulent tubes. Disc florets 7–20; corollas yellow, weakly bilabiate, glandular-puberulent below. Achenes of ray and disc similar, cylindric to clavate, black or dark brown, with a very small carpopodium, strigillose with short, uncinate trichomes. Pappus of 1–6 stout, retrorsely-barbed awns, or sometimes reduced to a low crown in the disc florets.

DISTRIBUTION: Central Sonora to Baja California Sur and northern Sinaloa from sea level to ca 500 m. One species, *P. coulteri*, occurs on the mainland areas of Sonora and Sinaloa; the other species, *P. multiseta,* is restricted to the southern portion of the Baja California peninsula (fig. 1). The disjunction between Baja California and the mainland is not unique to sect. *Heteropectis.* Six other species or species pairs within the genus have similar disjunctions, and a seventh has a continuous ditribution from the mainland to the peninsular region. For most of these

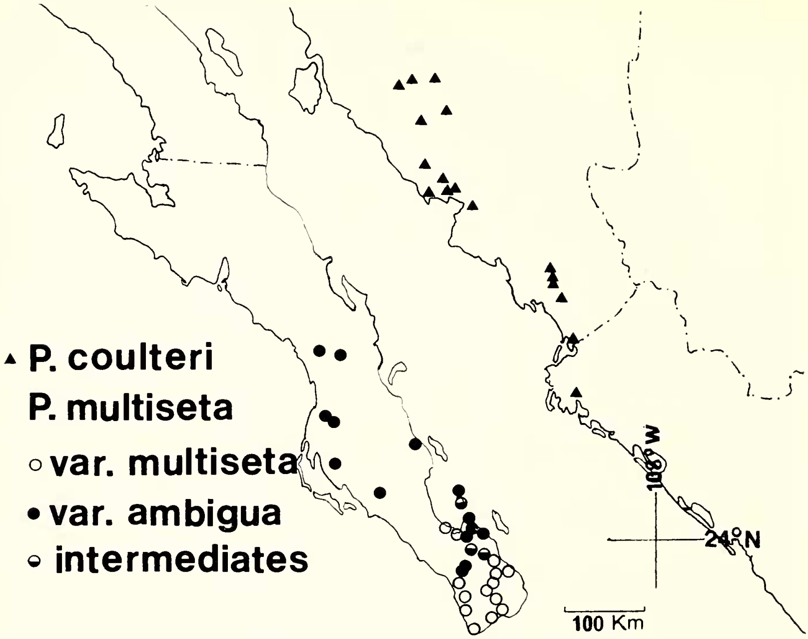


FIG. 1. Geographical distribution of *Pectis* sect. *Heteropectis*.

taxa, the mainland area appears to be the primary range of distribution. For sect. *Heteropectis*, with only two species, a certain determination of the primary range does not appear to be possible.

Key to *Pectis* sect. *Heteropectis*

1. Disc corollas bearing a sessile oil gland just below the apex of each tooth; some or all of the disc achenes often lacking an aristate pappus; plants of Baja California Sur. . . . . (2)
   2. Larger leaves usually 2–4 mm wide, bristly-serrate over most of their length; disc florets mostly 11–16; phyllaries imbricate. 1a. *P. multiseta* var. *multiseta*
   2. Larger leaves less than 2 mm wide, bearing bristles only below the middle; disc florets usually 7–12; phyllaries not imbricate. 1b. *P. multiseta* var. *ambigua*
1. Disc corollas eglandular; disc achenes all bearings a pappus of 2–6 awns; plants of Sonora and Sinaloa. . . . . . 2. *P. coulteri*

1. PECTIS MULTISETA Benth., Bot. Voy. Sulphur 20. 1844. TYPE: Mexico, Baja California Sur, Cape San Lucas, without date, *R. B. Hinds s. n.* Holotype: K, not seen; Isotype: US!

Much-branched, often medicinally-scented, tap-rooted annual herbs

(sometimes persisting for more than one growing season). Stems 1–30 cm long, prostrate to ascending, solitary or more commonly several from the base, few- to many-branched above, often pseudodichotomous, stramineous to reddish or purplish, densely puberulent. Leaves linear to oblanceolate, 2–35 mm long, 0.5–4.0 mm wide, mucronate or bristle-tipped, punctate on the undersurface with scattered oil glands ca 0.1 mm diameter. Heads solitary or in leafy cymose clusters. Peduncles slender, puberulent. Involucres cylindric to campanulate. Phyllaries linear-oblanceolate to obovate, 3.5–7.0 mm long, 1–2 mm wide, strongly convex, round-keeled, punctate near the margins and along the midrib with linear-elliptic to oval oil glands, ciliolate on the margins toward the apex. Ray florets 5; corollas yellow or often tinged with red, 4.0–8.5 mm long, often punctate with one to several small oil glands, glandular-puberulent on the tube. Disc florets 1–20; corollas yellow, 2.5–4.0 mm long, equally or subequally 5-toothed, with each tooth punctate just below the apex with an oval oil gland, with the tube glandular puberulent. Achenes 2.5–4.5 mm long. Ray and disc pappus similar, of 1–4 retrorsely-barbed awns 1–2 mm long, or the pappus of some or all of the disc achenes reduced to a low crown.

Pectis multiseta occurs in the southern portions of Baja California Sur where it grows in a variety of dry, open habitats from sea level to ca 500 m (fig. 1). As presently treated, this species is restricted to the southern tip of the peninsula; var. *ambigua* is more northern in distribution and extends into some of the drier areas of the Sonoran Desert.

1a. PECTIS MULTISETA Benth. var. MULTISETA.

Pectis bennettii Klatt, Leopoldina 25:108. 1899. TYPE: Mexico, Baja California Sur, Prom. St. Lucas, without date, *Bennett 21.* Holotype: B (destroyed), photograph of holotype, F! US!; Isotype: GH!; Lectotype (here chosen): GH.

Stems 3–30 cm long. Leaves 5–35 mm long, 1–4 mm wide, serrate to above the middle and often to the apex with bristle-tipped teeth, glabrous or sparsely puberulent on the margins and midrib beneath. Heads solitary or in open cymose clusters. Peduncles 1–4 cm long. Involucres campanulate. Phyllaries imbricate, obovate, 3.5-5.5 mm long, 1–2 mm wide, broadly rounded, very obtuse, narrowly hyaline-margined, glabrous or puberulent. Ray corollas 6.0–8.5 mm long, with ovate lingules 5–7 mm long and 2–4 mm wide. Disc florets 11–20; corollas 3–4 mm long, equally 5-toothed or slightly bilabiate. Achenes 2.5–4.5 mm long. Pappus awns 1–2 mm long. Chromosome number: $n = 12$. Flowering from September to May following seasonal rainfall. Fig. 2.

REPRESENTATIVE SPECIMENS: Baja California Sur: 19.2 mi SW of San Jose del Cabo, 17 Dec 1947, *Carter, Alexander, and Kellogg 2241* (F, GH, MO, US); San Jose del Cabo, 23 Jan 1928, *Jones 24054* (ARIZ, F, GH, MO, NY, SD, TEX, UC); Buenavista, 6 Jan 1959, *Moran 6904* (ARIZ, CAS, GH, SD, TEX); 6.4 mi N of Todos Santos, 26 Dec 1958, *Porter 77* (ARIZ, CAS, GH, TEX, UC, US); Arroyo

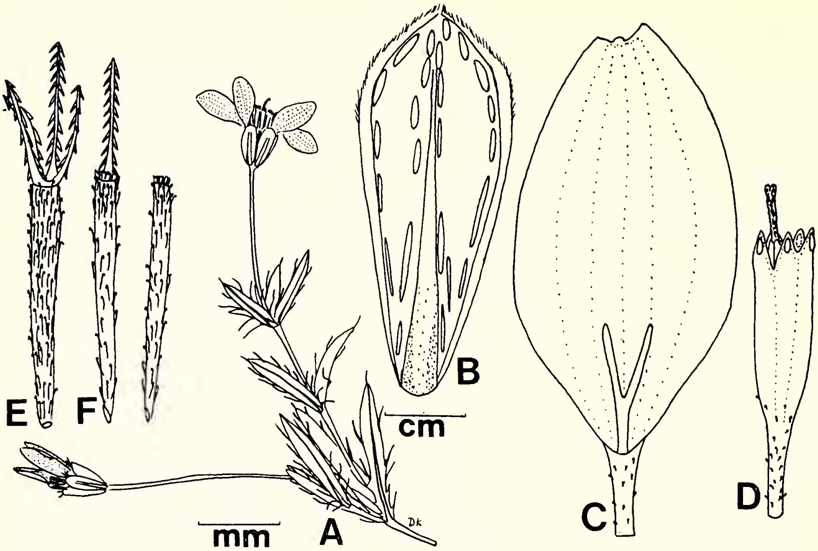


FIG. 2. *Pectis multiseta* var. *multiseta*. A, habit (*Dawson 1155*, F); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achenes. B–F, same scale (*Porter 77*, TEX).

Salado, Jan–Mar 1901, *Purpus 387* (ARIZ, MO, UC, US); between Miraflores and San Jose del Cabo, 6–7 May 1931, *Wiggins 5672* (CAS, GH, LL, NY, UC, US); 39.5 mi S of La Paz, 24 Dec 1958, *Wiggins 14513* (ARIZ, CAS, UC); Cape San Lucas, Aug 1859–Jan 1860, *Xantus 44* (GH, NY, US).

Variety *multiseta* is quite common in the Cape Region of Baja California Sur and frequently grows nearly to the water's edge along the seashore; inland, the plants of this variety are scattered in open areas of the thorn forest and in disturbed sites.

1b. **Pectis multiseta** Benth. var. **ambigua** (Fern.) Keil, comb. et stat. nov.—*Pectis ambigua* Fern., Proc. Amer. Acad. Arts 33:84. 1897. Syntypes: Mexico, Baja California Sur, San Gregorio, Sep 1889, *T. S. Brandegee s.n.* (Syntype: GH!; Isosyntypes: UC! US); La Paz, 20 Jan–5 Feb 1890, *E. Palmer 23* (Syntype: GH!; Isosyntypes: NY (2)! US!); Lectotype (here chosen): *E. Palmer 23* (GH!).

Stems 1–20 cm long. Leaves 2–20 mm long, 0.5–2.0 mm wide, one to several setose-toothed, usually only below the middle, glabrous or puberulent on one or both surfaces. Heads solitary or in more-or-less congested cymose clusters. Peduncles 2–20 mm long. Involucres cylindric or narrowly campanulate. Phyllaries not or scarcely imbricate, linear-oblong, 3.5–7.0 mm long, 1.0–1.5 mm wide, very convex, very narrowly hyaline-margined, glabrous to densely puberulent. Ray corollas 4.0–6.5 mm long, with ovate ligules 1.0–2.5 mm wide. Disc florets 7–12; corollas

2.5–4.0 mm long, weakly bilabiate, with the narrow lobe ca twice the length of the teeth on the broad lobe. Achenes 3–4 mm long. Pappus awns 1 mm long. Chromosome number: $n = 12$. Flowering October to May following seasonal rains. Fig. 3.

Representative specimens: Baja California Sur: SE of La Paz on rd to Puente Coyote, 31 Mar 1949, *Carter 2603* (GH, US); Arroyo de Bachomo, 21 Mar 1973, *Carter et al. 5794* (UC); La Paz, 30 Mar 1931, *Collins, Kearney, and Kempton 57* (F, LL); 5.6 mi N of La Paz, 7 Oct 1964, *Hastings and Turner 64–139* (SD); 22 mi SW of Comundu, 18 Mar 1935, *Shreve 7134* (ARIZ, F, MO, UC, US); 13 mi N of El Refugio, 19 Mar 1935, *Shreve 7173* (ARIZ, F, UC, US); NW of El Triunfo, 29 Apr 1959, *Thomas 7690* (US); near Queretaro, 28 Apr 1931, *Wiggins 5514* (GH, LL, UC, US).

Two lines of evidence support the reduction of *Pectis ambigua* to varietal status within *P. multiseta*. In the area of sympatry between the two taxa, populations containing intermediate individuals are indicative of hybridization (e.g., *Wiggins 15339*, TEX). Additionally, populations of var. *ambigua* exhibit a clinal variation in leaf size and shape. The leaves in the southernmost populations are larger and bear more mar-

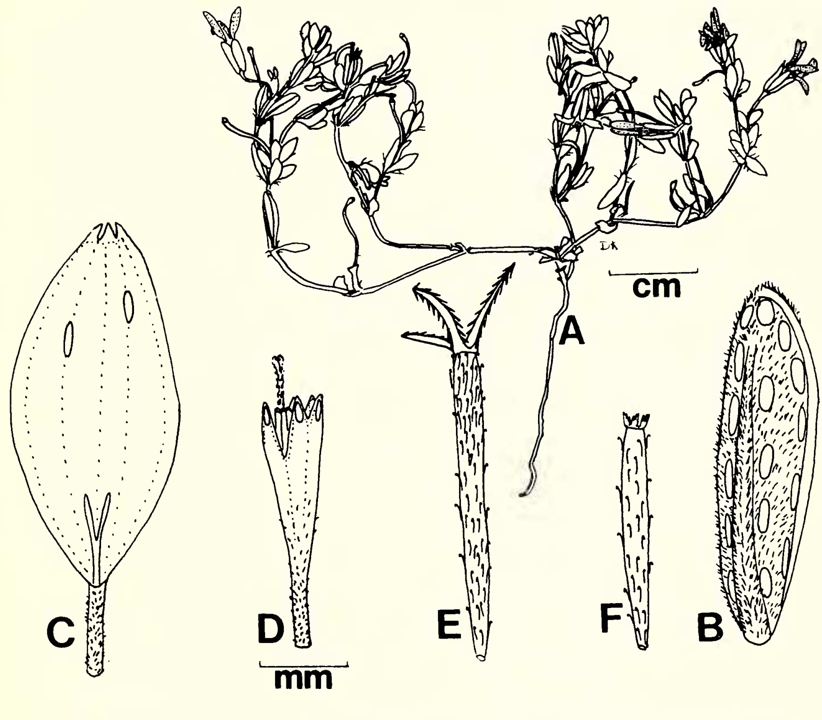


Fig. 3. *Pectis multiseta* var. *ambigua*. A, habit (*Wiggins 5514*, US); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achene. B–F, same scale (*Sikes and Babcock 261*, TEX).

ginal bristles than those in the northern populations. This variation apparently represents introgression between the southern populations of var. *ambigua* and the larger-leaved var. *multiseta.*

2. Pectis coulteri Harv. & Gray in A. Gray, Mem. Amer. Acad. Arts 4:62. 1849. Type: "California" (probably actually collected in Sonora near Hermosillo or Guaymas), without date, *T. Coulter 331.* Holotype: TCD, not seen; Isotype (fragmentary): GH!

Plants bushy, medicinally-scented, tap-rooted, annual herbs (sometimes persisting through more than one growing season). Stems 5–35 cm long, solitary or more commonly several to many from near the base, pseudodichotomously branching above, stramineous or reddish-tinged, densely puberulent. Leaves linear, 5–30 mm long, 0.5–1.5 mm wide, mucronate, tapering slightly toward the base, with one or two pairs of setose-tipped basal teeth, otherwise entire, punctate on the margins with rounded oil glands up to 0.2 mm diameter and occasionally with a few scattered glands on the undersurface, glabrous to densely puberulent. Heads in open to condensed cymose clusters, Peduncles 5–20 mm long, densely puberulent. Involucres cylindric to very narrowly campanulate. Phyllaries 5, oblong to narrowly obovate, 4–7 mm long, 1.0–1.7 mm wide, strongly convex, keeled nearly to the tip, truncate at the base, gibbous, weakly longitudinally striate, very narrowly hyaline- or purplish-margined, dotted along the margin and along the upper half of the midrib with rounded oil glands up to 0.5 mm diameter, densely villous-ciliolate along the margins, glabrous to puberulent on the back. Ray florets 5; corollas yellow or sometimes becoming reddish-tinged, 6–8 mm long, with oblong to ovate ligules 5–7 mm long and 2–3 mm wide, sparsely glandular-puberulent on the tube below. Disc florets 10–15; corollas yellow, 3.0–3.5 mm long, weakly bilabiate, with the narrow lobe 1–2 mm long, 2–3 times the length of the triangular glandless teeth on the broad lobe, glandular-puberulent on the tube. Achenes 3.5–4.0 mm long. Pappus of ray and disc similar, of 2–6 retrorsely-barbed awns 1–2 mm long. Chromosome number: $n = 12$. Flowering much of the year except during the driest summer months. Fig. 4.

Representative specimens: Sinaloa: 0.5 mi N of Topolobampo, 29 Dec 1963, *D. Flyr 71* (TEX); Topolobampo, 23 Mar 1910, *Rose, Standley, and Russell 13273* (US). Sonora: near Navojoa, 27 Oct 1939, *Gentry 4751* (ARIZ, MO, NY, UC); 28 m S of Hermosillo, 7 Sep 1971, *Keil and Canne 8602* (OS); 27 mi SE of Navojoa, 10 Sep 1971, *Keil and Canne 8734* (OS); Guaymas, 1887, *Palmer 143* (GH, NY, UC, US); Agiabampo, Oct 1890, *Palmer 759* (GH, MO, NY, UC, US); Torres, Jan-Mar 1902, *Purpus 416* (MO, UC, US); vicinity of Empalme, 11 Mar 1910, *Rose, Standley, and Russell 12632* (F, GH, MO, NY, US); 12 mi W of Hermosillo, 27 Aug 1941, *Wiggins and Rollins 122* (ARIZ, GH, LL, MO, NY, UC, US).

Pectis coulteri occurs from central Sonora to northern Sinaloa from

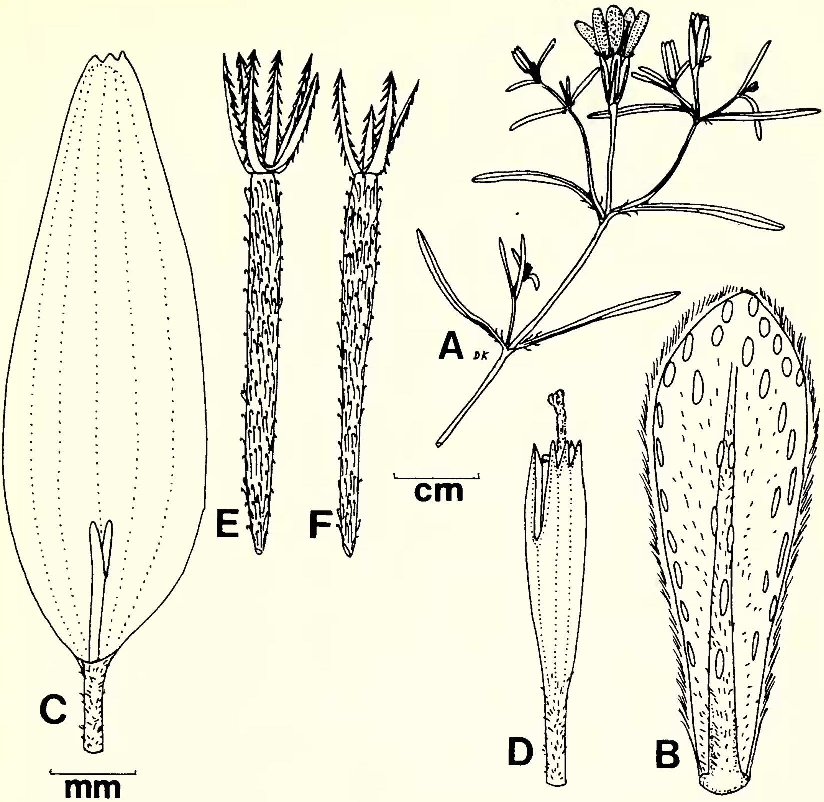


FIG. 4. *Pectis coulteri.* A, habit (*Keil and Canne 8728,* US); B, phyllary; C, ray corolla; D, disc corolla; E, ray achene; F, disc achene. B–F, same scale (*Keil and Canne 8730,* OS).

sea level to ca 500 m (fig. 1). Various authors (Gray, 1884; Fernald, 1897; Rydberg, 1916; Kittell, 1941; Kearney and Peebles, 1960; Shreve Wiggins, 1964) have also included southern Arizona within the range of *P. coulteri.* I believe that this inclusion is erroneous and that it represents the perpetuation of an old error. Two collections have apparently been the basis for listing *P. coulteri* in the flora of Arizona: (1) an early collection by Edward Palmer labeled "Arizona" without locality (GH); and (2) the type collection of *P. coulteri.*

The veracity of the label data on some of Edward Palmer's early collections from western North America has been challenged previously. McVaugh and Kearney (1943) list several instances of mislabeled specimens that Palmer supposedly had found in Arizona but actually had collected in other regions. This apparently is the situation in the case of *P. coulteri.* Palmer probably collected *P. coulteri* in Sonora rather than in Arizona during an 1869 trip from Tucson, Arizona, to Guaymas,

Sonora. Indeed, there is a collection of *P. coulteri* in US collected by Palmer in 1869 in Sonora with "Arizona" penciled on the label above "Sonora".

The locality for the type collection of *P. coulteri* is also confused. Thomas Coulter collected specimens of three different species of *Pectis* that were later described as new by Harvey and Gray (in Gray, 1849). All three, *P. coulteri, P. filipes*, and *P. papposa,* bear labels indicating that they had been collected in California (without localities or dates). Neither *P. coulteri* nor *P. filipes,* is known to grow in California, and this was recognized by Gray, himself (1884), who suggested that Coulter had collected the specimens in Arizona. Coville (1895) in documenting Coulter's 1832 trip to the mouth of the Gila River in Arizona added his support to the argument that Coulter had collected the type of *P. coulteri* in Arizona. In the same publication, however, Coville mentioned the case of *Berginia virgata* Benth. & Hook. (Acanthaceae), originally described from one of Coulter's "California" collections, later attributed to Arizona, and finally rediscovered in Sonora [and still known only from Mexico (Shreve and Wiggins, 1964)]. Keil (1973) has shown that a similar situation is true for *Pectis filipes,* for which the typical variety is wholly Mexican.

Coulter collected in Sonora in the vicinity of Hermosillo and Guaymas (Coville, 1895; McVaugh, 1943), areas where *P. coulteri, P. filipes,* and *P. papposa* are all common. It is in these regions that I believe he gathered the types for these species. Consequently, unless and until the occurrence of *Pectis coulteri* in Arizona can be documented with certainty, I feel that this species should be excluded from the known flora of Arizona.

The 1869 collection of *P. coulteri* by Edward Palmer (*s.n.,* US) that was mentioned above is morphologically peculiar. Unlike all other specimens of *P. coulteri* that I have examined, the single plant on this sheet has heads with 13 ray florets! Correlated with this feature are greater than usual numbers of disc florets and phyllaries much narrower than usual. I know of no other case in *Pectis* of a typically 5-rayed species having such an abnormality.

Acknowledgments

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REPRODUCTIVE BIOLOGY OF GOODYERA OBLONGIFOLIA (ORCHIDACEAE)

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Discovery of a large population of *Goodyera oblongifolia* Raf. prompted this investigation. Since some northern temperate orchids are known to have replaced or supplemented allogamy (cross-pollination) with autogamy (self-pollination) and asexual reproduction, the question arose as to what adaptations contributed to the success of the study population. Interrelations of vegetative propagation, self-compatibility, seed fertility, flower aggregation, nectar production, capsule development, pollination mechanisms, and pollinator distributions are considered.